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A new species of *Cristaria* Schumacher, 1817 (Bivalvia, Unionidae) from Sichuan, China

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Abstract

The species diversity of freshwater mussels in the upper Yangtze River has been seriously underestimated, and human-induced disturbances have severely threatened the survival of local bivalve species. In this study, we describe a new freshwater mussel species, *Cristaria wangyucheni* Z.-G. Chen & Y.-T. Dai, **sp. nov.**, from the Jialing River Basin in the upper Yangtze River, Sichuan, China, based on comparative morphology and molecular phylogeny. Phylogenetic analyses of *COI* and *28S* rRNA gene fragments revealed that *C. wangyucheni* **sp. nov.** is a sister to the other species of *Cristaria*. The pairwise uncorrected *COI p*-distance analysis demonstrated genetic distances ranging from 10.10% (between this species and *C. truncata*) to 13.17% (between this species and *C.* "*beirensis*"). Morphologically, *C. wangyucheni* **sp. nov.** can be distinguished from its congeners by its medium-sized shell, which ranges from an elongated triangle to an irregular rectangle. This discovery broadens our understanding of interspecific shell morphological variation within the genus *Cristaria*.

Key Words

Freshwater mussel, morphology, phylogeny, taxonomy, upper Yangtze River Basin

Introduction

Freshwater mussels (Bivalvia, Unionida) comprise six families with 214 genera and 998 recent species worldwide, of which the Unionidae are especially diverse in Asia, accounting for over 30% of all described species (Graf and Cummings 2025). China is the center of freshwater mussel distribution in East Asia, harboring an exceptionally high diversity of endemic species (Zieritz et al. 2018; Liu et al. 2022). The recent discovery of numerous new species in this region indicates that the diversity of freshwater mussels has been substantially underestimated, particularly in areas of China that have received limited attention in the past, such as the Pearl River Basin and the upper Yangtze River Basin (Wu et al. 2022; Dai et al. 2023; Liu et al. 2023; Dai et al. 2024a; Liu et al. 2024; Wu et al. 2024; Chen et al. 2025; Hou et al. 2025).

The genus *Cristaria* Schumacher, 1817, the type taxon of the subtribe Cristariina Lopes-Lima, Bogan & Froufe, 2017 within the family Unionidae Rafinesque, 1820, is characterized by large, flat, triangular shells, a well-developed post-dorsal wing, and vestigial pseudocardinal and lateral teeth (Liu et al. 1979; He and Zhuang 2013). This genus is widely distributed across East, Northeast,

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and Southeast Asia and is particularly widespread in China, occurring in almost all river basins in the eastern regions of the country (Haas 1969; Brandt 1974; He and Zhuang 2013; Klishko et al. 2014; Klishko et al. 2016; Wu et al. 2025; Graf and Cummings 2025). Notably, *Cristaria* holds significant economic value, with *Cristaria plicata* (Leach 1814) being particularly prominent. This species is one of the main producers of freshwater pearls, which are highly prized in China's aquaculture industry and are commercially known as "freshwater pearl mussels" (Liu et al. 1979; Wen et al. 2006). However, taxonomic studies on this group have primarily focused on the Far East (Klishko et al. 2014; Klishko et al. 2016; Lopes-Lima et al. 2020), while domestic research remains relatively scarce (Wu et al. 2025). Recently, Wu et al. (2025) conducted an integrative taxonomic and mitochondrial phylogenomic analysis of the subtribe Cristariina Lopes-Lima, Bogan & Froufe, 2017 in *Cristaria truncata* Dang, Thai & Pham, 1980, which was newly recorded in China, being discovered in the Pearl River Basin in Nanning, Guangxi. Consequently, four species of this genus are recognized in China: *Cristaria beirensis* Liu & Zhang, 1982; *Cristaria plicata* (Leach, 1814); *Cristaria radiata* Simpson, 1900; and *Cristaria truncata* Dang, Thai & Pham, 1980 (Wu et al. 2025).

During surveys conducted in 2025, we discovered a group of freshwater mussels from the upper Yangtze River with peculiar shells that did not resemble any known species. Using an integrative approach that combined shell morphology with phylogenetic analyses of *COI* and *28S* rRNA genes, we confirmed this lineage as a new species of *Cristaria*. Our findings provide further evidence that species diversity in the upper Yangtze River Basin is underestimated, highlighting the need for more comprehensive field studies in the region.

Materials and methods

Specimens were collected in Sichuan Province, China, in March and June of 2025 (Figs 1, 2). Living specimens were initially frozen at −20 °C for 24 hours and subsequently thawed at room temperature for 2 hours to facilitate the extraction of soft parts. The soft parts were then fixed in 70% ethanol. Empty shells were cleaned, dried, and preserved at room temperature. Photographs were taken using a Sony A7CII.

Total genomic DNA was extracted from foot tissue preserved in 70% ethanol using the TIANamp Marine Animals DNA Kit (Tiangen Biotech, China). We amplified and sequenced fragments from the mitochondrial cytochrome c oxidase subunit-I gene (*COI*) (LCO22 me2 + HCO700dy2) (Walker et al. 2007) and the nuclear 28S ribosomal RNA gene (*28S*) (D23F + D4RB) (Park and Foighil 2000). The polymerase chain reaction (PCR) was conducted using a 25 μL mixture of 2 × Taq Plus Master Mix II (Vazyme, China) (12.5 μL), ddH_2O (9.5 μL), 10 μM primers (1 μL each), and genomic DNA (1 μL, about 100 ng/μL). Thermal cycling was started at 98 °C for 10 s, followed by

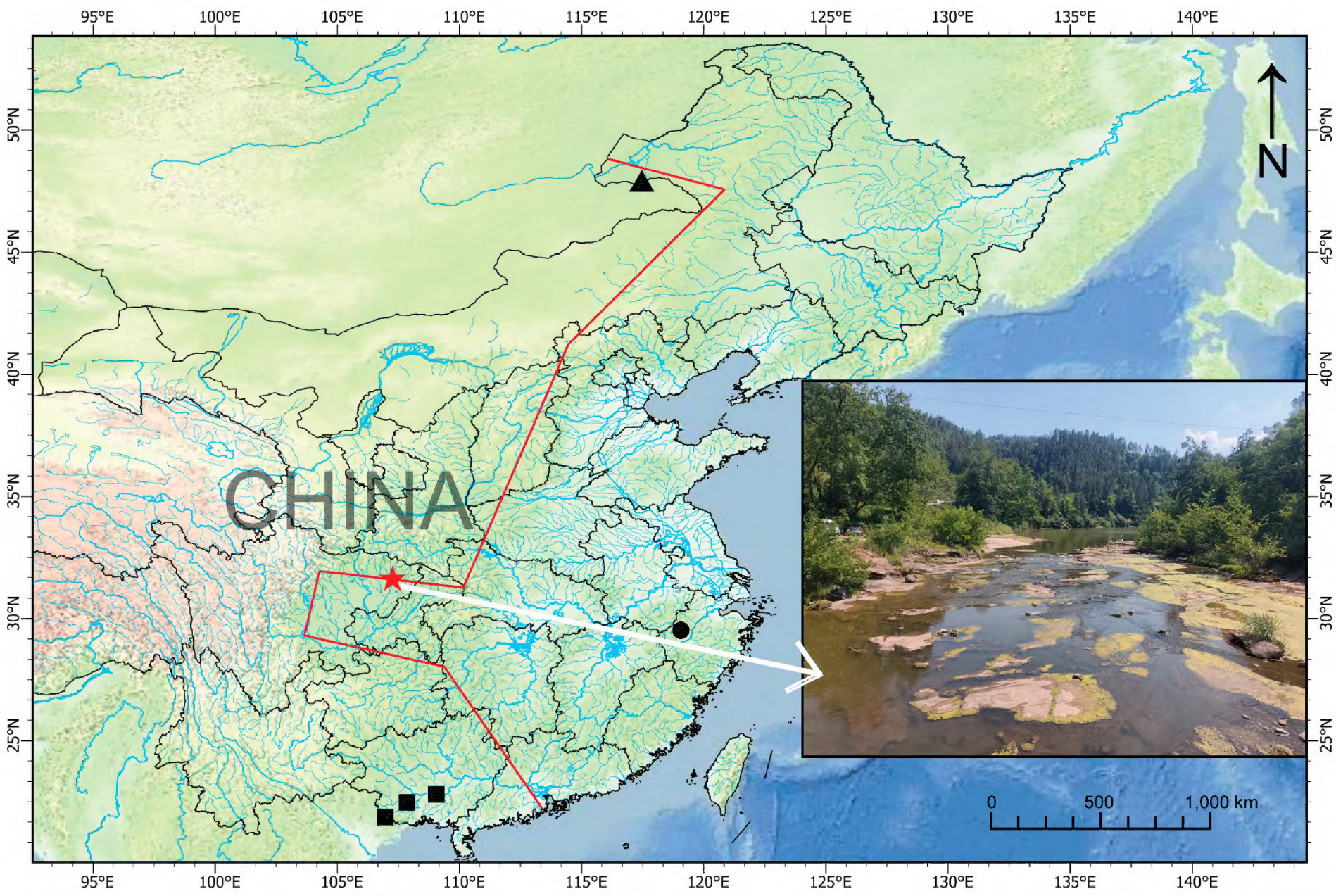

Figure 1. Distribution of *Cristaria* in China. East of the red line. *C. plicata*; *C. wangyucheni* sp. nov. (red star); *C. beirensis* (black triangle); *C. truncata* (black square); *C. radiata* (black circle).

35 cycles of 94 °C for 1 min, annealing at 50 °C for 1 min, and extension at 72 °C for 1 min, and then a final extension at 72 °C for 7 min. The PCR products were sequenced commercially by Sangon Biotech (Shanghai, China). The newly obtained sequences have been deposited in GenBank, and their accession numbers are provided in Table 1.

Table 1. GenBank accession numbers of sequences used in this study.

Taxon	*COI*	*28S* rRNA	Country
UNIONIDAE Rafinesque, 1820			
Unioninae Rafinesque, 1820			
Cristariini Lopes-Lima, Bogan, & Froufe, 2017			
Cristaria wangyucheni sp. nov. 1	PX353907	PX352028	China
Cristaria wangyucheni sp. nov. 2	PX353908	PX352029	China
C. bellua (Morelet, 1866) 1	ON704642	ON695893	Laos
C. bellua (Morelet, 1866) 2	ON704643	ON695894	Laos
C. bellua (Morelet, 1866) 3	ON704644	ON695895	Laos
C. bellua (Morelet, 1866) 4	ON704645	ON695896	Laos
C. clessini (Kobelt, 1879) 1	MT020592	MT020810	Japan
C. clessini (Kobelt, 1879) 2	MT025813	n/a	Japan
C. clessini (Kobelt, 1879) 3	MT025814	n/a	Japan
C "beirensis" Liu &Zhang, 1982 1	PQ387017	n/a	China
C "beirensis" Liu &Zhang, 1982 2	PQ387018	n/a	China
C. plicata (Leach, 1814) 1	MG462956	MG595484	China
C. plicata (Leach, 1814) 2	EU698947	MG595485	China
C. plicata (Leach, 1814) 3	EU698948	MG595486	China
C. plicata (Leach, 1814) 4	EU698949	MG595487	China
C. radiata Simpson, 1900 1	EU698909	n/a	China
C. radiata Simpson, 1900 2	EU698910	n/a	China
C. radiata Simpson, 1900 3	EU698937	n/a	China
C. truncata Dang, Thai & Pham, 1980 1	OP491287	OP499826	Vietnam
C. truncata Dang, Thai & Pham, 1980 2	OP491288	OP499827	Vietnam
C. truncata Dang, Thai & Pham, 1980 3	OP491289	n/a	Vietnam
C. truncata Dang, Thai & Pham, 1980 4	OP491290	n/a	Vietnam
Amuranodonta kijaensis Moskvicheva, 1973	MK574204	MK574473	Russia
Anemina arcaeformis (Heude, 1877)	MG462936	MG595463	China
Beringiana beringiana (Middendorff, 1851)	MT020557	MT020799	Japan
B. japonica (Clessin, 1874)	MT020576	MT020803	Japan
B. fukuharai San, Hattori & Kondo, 2020	MT020567	MT020801	Japan
B. gosannensis San, Hattori & Kondo, 2020	MT020584	MT020802	Japan
Buldowskia flavotincta (Martens, 1905)	MT020537	MT020804	South Korea
B. suifunica (Lindholm, 1925)	MK574190	MK574460	Russia
B. iwakawai (Suzuki, 1939)	MT020523	MT020806	Japan
B. kamiyai San, Hattori & Kondo, 2020	MT020525	MT020808	Japan
B. shadini (Moskvicheva, 1973)	MK574197	MK574467	Russia
*Plethol*ophus *honglinhensis* Bogan, Do, Froufe & Lopes-Lima, 2023	OR912962	OR913009	Vietnam
P. reinianus (Martens, 1875)	MT020603	n/a	Japan
P. tenuis (Griffith & Pidgeon, 1833)	KX822658	KX822614	Vietnam
P. tenuis (Griffith & Pidgeon, 1833)	MT020599	LC519084	Japan
P.s tenuis (Griffith & Pidgeon, 1833)	MT020600	LC519085	Japan
P. tenuis (Griffith & Pidgeon, 1833)	MT020601	KX822614	Japan
P. tenuis (Griffith & Pidgeon, 1833)	MT020602	KX822614	Japan
P. guangzhouensis Dai, Chen, Huang & Wu, 2024	PP945818	PP956591	China
P. guangzhouensis Dai, Chen, Huang & Wu, 2024	PP945819	PP956591	China
P. guangzhouensis Dai, Chen, Huang & Wu, 2024	PP945820	PP956591	China
P. guangzhouensis Dai, Chen, Huang & Wu, 2024	PP945821	PP956591	China
Sinanodonta angula (Tchang, Li & Liu, 1965)	MG463053	MG595580	China
S. calipygos (Kobelt, 1879)	MT020623	MT020833	Japan
S. lauta (Martens, 1877)	MT020616	MT020834	Japan
S. lucida (Heude, 1877)	MG463066	MG595589	China
S. schrenkii (Lea, 1870)	MT020618	MT020837	South Korea
S. tumens (Haas, 1910)	MT020622	MT020838	Japan
S. pacifica (Heude, 1878)	MG463052	MG595599	China
S. woodiana (Lea, 1834)	MG463080	MG595608	China
Parreysiinae Henderson, 1935			
Scabies crispata (Gould, 1843)	MG288632	MG552824	Thailand
Trapezidens exolescens (Gould, 1843)	KX230532	KX230559	Thailand
MARGARITIFERIDAE Henderson, 1929			
Gibbosula laosensis (Lea, 1863)	JX497731	KT343741	Laos
Margaritifera margaritifera (Linnaeus, 1758)	KX550089	KX550093	Russia

Two datasets were constructed in this study: (i) the *COI* dataset (36 sequences; 615 bp) and (ii) the *COI* + *28S* rRNA dataset (49 sequences; 1,023 bp) (Table 1). The *COI* sequences were aligned using MEGA X (Kumar et al. 2018), and the 28S sequences were aligned using MAFFT v. 7 (Katoh et al. 2019) using the Q-INS-i algorithm. The best-fit model for each gene and gene partition was calculated by PartitionFinder2 v. 1.1 (Lanfear et al. 2017), based on the corrected Akaike Information Criterion (AICc) and using a heuristic search algorithm. The program proposed the division of the concatenated dataset into two partitions, comprising partitions for each of the three codon positions of the *COI* gene and the 28S gene. The best-fit model was determined to be GTR+I+G for the first and second codon positions of *COI*, while GTR+G was selected for the third position of *COI* and the 28S gene.

Bayesian inference (BI) and maximum likelihood (ML) analyses were performed using MrBayes ver. 3.2.6 (Ronquist et al. 2012) and IQ-TREE ver. 2.2 (Nguyen et al. 2015). Two species of Margaritiferidae Henderson, 1929, and Parreysiinae Henderson, 1935, respectively, were used as the outgroups for rooting the trees. For the Bayesian analysis, four independent Markov Chain Monte Carlo (MCMC) runs were performed simultaneously for 10 million generations, with trees sampled every 1,000 generations and the first 25% discarded as burn-in. Convergence was assessed based on an average standard deviation of split frequencies < 0.01 and a potential scale reduction factor (PSRF) close to 1. Node support for maximum likelihood analysis was determined using 1000 rapid bootstrap (BS) replicates. Trees were visualized in FigTree v. 1.4.3 (http://tree.bio.ed.ac.uk/software/figtree/).

Abbreviations. **JXAU:** Jiangxi Agricultural University (Nanchang, Jiangxi, China); **aam:** anterior adductor muscle; **pam:** posterior adductor muscle; **ea:** excurrent aperture; **ia:** incurrent aperture; **pia:** papillae of the incurrent aperture; **pea:** papillae of the excurrent aperture; **ig:** inner gills; **og:** outer gills; **m:** mantle; **lp:** labial palps; **vm:** visceral mass; **f:** foot.

Results

Phylogenetic analyses

In this study, molecular data were obtained from only two specimens of the new species. The *COI* dataset comprised 615 aligned positions, including 154 variable sites and 143 parsimony-informative sites. The concatenated *COI* + *28S* dataset, after trimming, consisted of 1,009 positions (600 bp of *COI* and 409 bp of *28S*), with 385 variable sites and 310 parsimony-informative sites.

The ML and BI trees based on the *COI* + *28S* dataset exhibited largely identical topologies, except for three nodes containing polytomies in the BI tree (Fig. 3). In both trees, *Cristaria* Schumacher, 1817, exhibited monophyly with the highest support (BS/BPP = 100/1.0). Furthermore, except for *C.* "*beirensis*" and *C. radiata*, which cluster together, all other species within the genus form a monophyletic clade. In the ML tree, specimens of *Cristaria* from the Tongbo River, Dazhou, Sichuan, form a distinct taxon and were recovered as sister to all other members of the genus (BS = 100). In the BI tree, however, there was a polytomy at this node. Pairwise uncorrected *COI p*-distance analysis demonstrated genetic distances between this species and other *Cristaria* species ranging from 10.10% (between this species and *C. truncata*) to 13.17% (between this species and *C.* "*beirensis*") (Table 1). It occupies a unique phylogenetic position and displays distinctive morphological characteristics (Figs 2, 3), which are described herein as *Cristaria wangyucheni* Z.-G. Chen & Y.-T. Dai, sp. nov.

Systematics

Family Unionidae Rafinesque, 1820
Subfamily Unioninae Rafinesque, 1820
Tribe Anodontini Rafinesque, 1820
Subtribe Cristariina Lopes-Lima, Bogan & Froufe, 2017
Genus *Cristaria* Schumacher, 1817

***Cristaria wangyucheni* Z.-G. Chen & Y.-T. Dai, sp. nov.**
https://zoobank.org/202187CD-AC6F-44E9-9A45-E6D92A25CF43
Fig. 2

Type materials. ***Holotype.*** • JXAU2503001 (collected alive, soft part stored in ethanol separately), Tongbo River [铜钵河], Qingning Town [青宁镇], Tongchuan District [通川区], Dazhou City [达州市], Sichuan Province, China, 31.50518°N, 107.40832°E, leg. Yu-Chen Wang, March 2025.

***Paratypes*:** n = 8, • JXAU2503002 (collected alive, soft parts stored in ethanol separately), • JXAU2503003–006 (empty shells), other information same as holotype; • JXAU2503007–009 (empty shells), leg. Zhong-Guang Chen & Yan-Shu Guo, June 2025, other information same as holotype.

Diagnosis. Shell elongated triangle to irregular rectangle, inflated, very thin, fragile, with a maximum length of about 100 mm. Postdorsal wing small and low.

Description. Shell medium size, thin, inflated, elongated, glossy, opaque. Post-dorsal wing small and low. Anterior small, rounded, and short; posterior expanded, wide, and long. Dorsal margin slightly curved downwards and truncated in behind; ventral margin weakly curved or retuse. Umbo inflated, slightly higher the hinge line, located at 1/4 of the dorsal margin, with concentric square carving. Periostracum yellowish green to brown with thin growth lines with a shallow sulcus in the middle of the dorsal margin. Growth lines arranged in irregular concentric circles. Hinge short. Ligament short and strong. Beak cavities shallow, open. Mantle attachment scars on the pallial line indistinct. Anterior adductor muscle scars oval, shallow, smooth; posterior adductor muscle scars oval, smooth. Pseudocardinal teeth completely degenerates and disappears. Lateral teeth of both valves short and thin. Nacre light white.

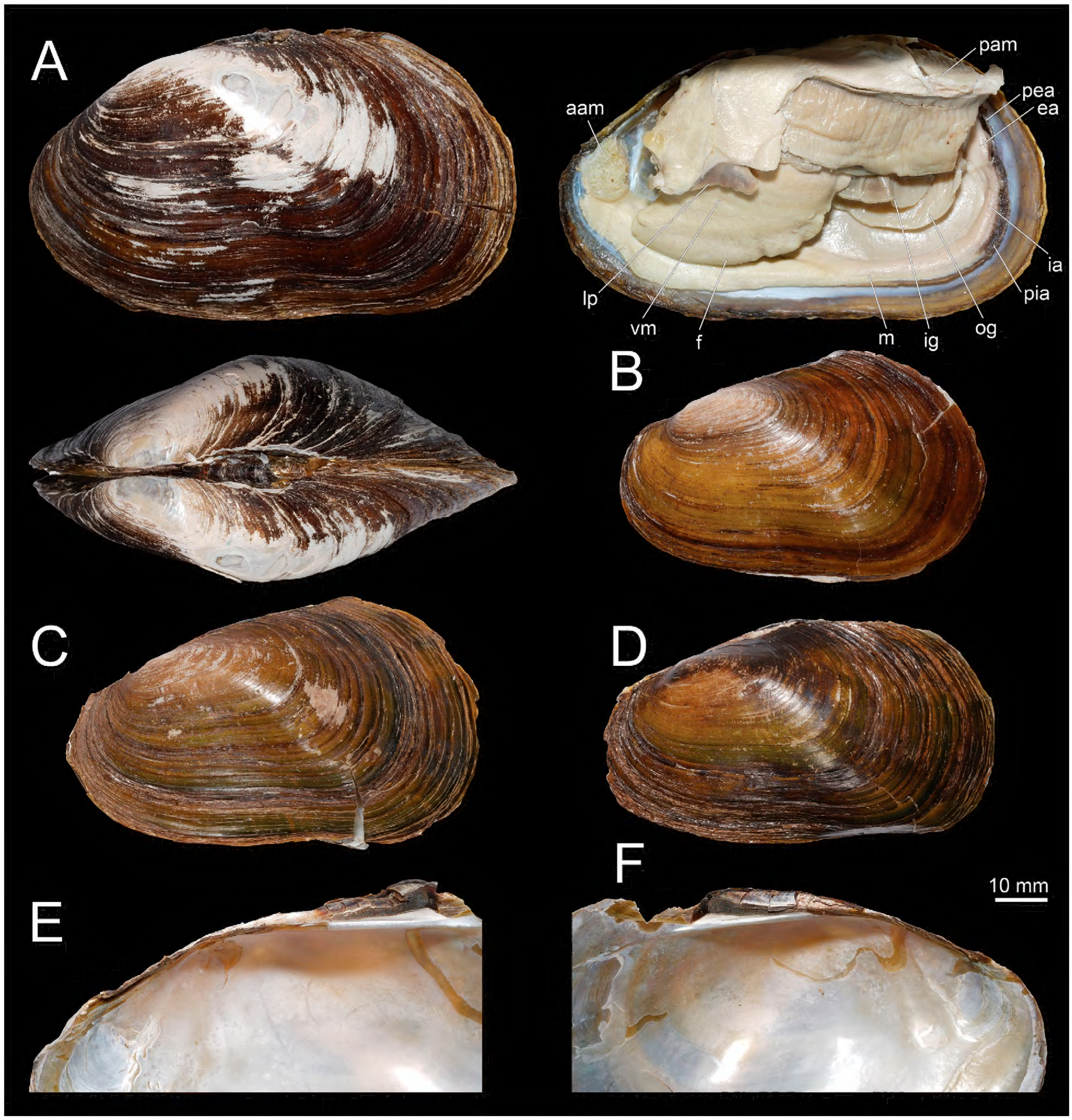

Figure 2. *Cristaria wangyucheni* sp. nov. **A.** Holotype, JXAU2503001; **B–F.** Partial paratypes, JXAU2503002, JXAU2503005, JXAU2503003, JXAU2503004, JXAU2503004.

Mantle light brown. aperture margins black, papillae of the excurrent aperture highly vestigial, papillae of the incurrent aperture weak. Gills light brown, inner gills slightly longer and wider than outer gills. Labial palps-rown, irregular triangle, distally pointed. Visceral mass grayish white. Foot grayish white.

Measurements. Holotype: shell length 95.1 mm, height 54.9 mm, width 42.0 mm. Paratypes: shell length 62.5–105.9 mm, height 41.8–61.9 mm, width 25.0–42.8 mm (Table 3).

Etymology. The species is named after Yu-Chen Wang, who first discovered it.

Vernacular name. 王氏冠蚌 (pīnyīn: wáng shì guàn bàng).

Distribution and ecology. Known from the type locality only (Fig. 1). Living in the pebble-bottom sections of the cold and flowing tributaries with seasonal floods, along with *Pseudocuneopsis* sp., *Nodularia* sp., and *Ptychorhynchus* sp. This species is considered to have a small population, as evidenced by multiple surveys that revealed a narrow distribution and a scarcity of live specimens.

Discussion

The pronounced morphological plasticity of freshwater mussels facilitates adaptation to diverse environments but complicates their taxonomic classification

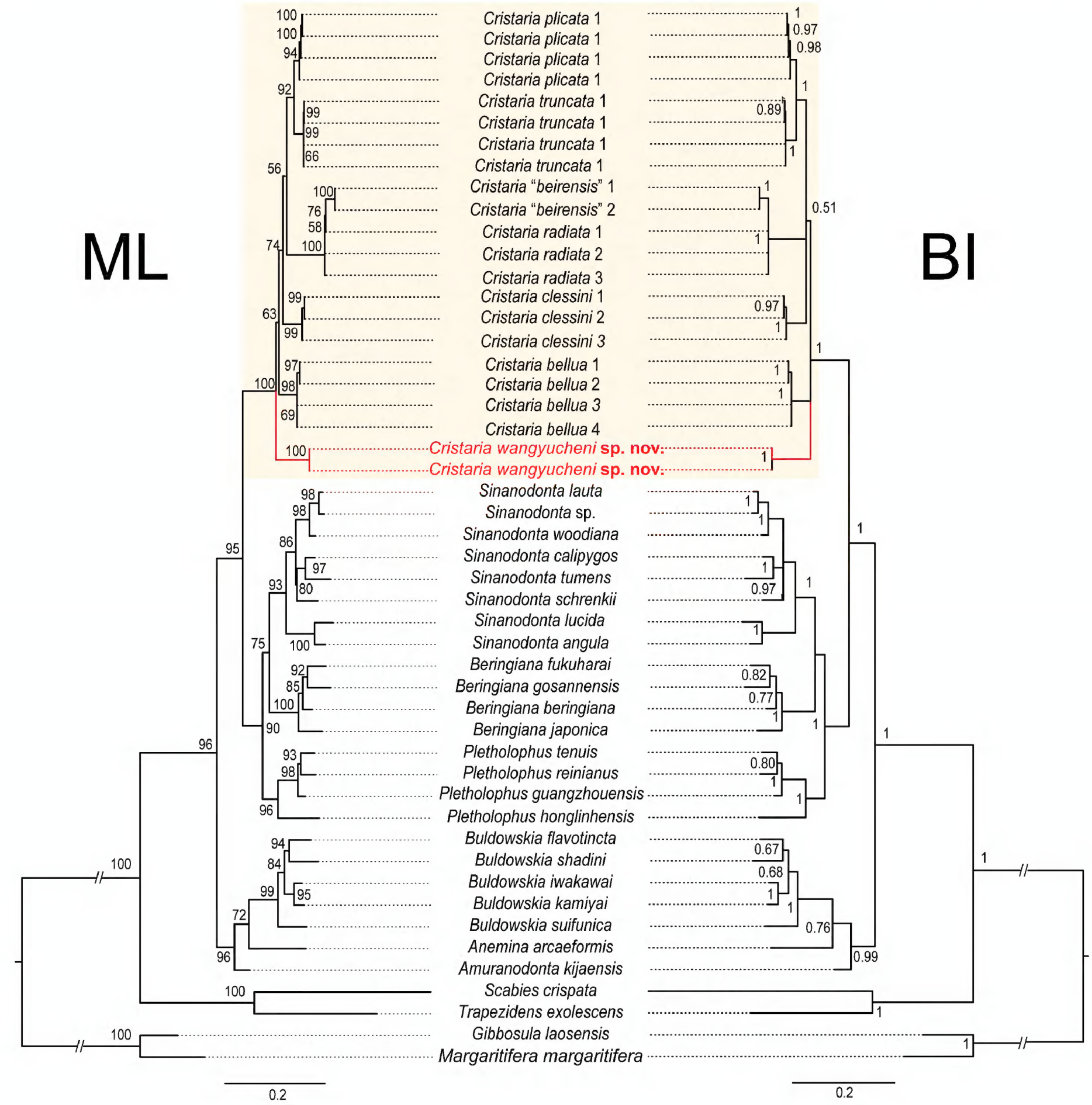

Figure 3. Maximum likelihood (ML) and Bayesian inference (BI) trees of Unionidae based on the *COI* + *28S* dataset. Support values above the branches are the posterior probability and bootstrap support, respectively.

(Inoue et al. 2013; Bogatov and Prozorova 2018; Dai et al. 2024b). In terms of shell morphology, *Cristaria wangyucheni* differs greatly from all congeners and is even difficult to place in the genus *Cristaria*. It can be distinguished from all congeners by the elongated triangle to irregular rectangle shell (vs. triangle) with a maximum length of about 100 mm (vs. 150–500 mm) and the small and low post-dorsal wing (vs. large and high) (Table 4). Detailed examination revealed that the pseudocardinal teeth are nearly degenerated and the lateral teeth are short, a condition resembling that of the genus *Cristaria* (Wu et al. 2025). In addition, this species can be distinguished by its inflated shell, an open umbo cavity, and a shallow sulcus in the middle of the dorsal margin, all of which represent important diagnostic characteristics (Table 4). Molecular phylogenetic analysis provides strong support for its recognition as a distinct species (Fig. 3). The interspecific genetic distances between this species and its congeners range from 10.10% to 13.17% (Table 2), far exceeding the widely recognized 3% threshold for interspecific divergence (Barrett and Hebert 2005), thereby providing strong evidence for its taxonomic distinctiveness. The discovery of the new species has expanded our understanding of the interspecific variations in shell morphology of the genus *Cristaria*. In the phylogenetic tree, *C.* "*beirensis*" and *C. radiata* cluster within the same clade, which is inconsistent with the species delimitation results of Wu et al. (2025) based on the *COI* gene. The specimen identified as *C. radiata* in Wu et al.

Table 2. Average intraspecific (bold) and interspecific uncorrected *p*-distance (% ± S.E.) for *COI* sequences of species in *Cristaria* Simpson, 1900.

Taxa	1	2	3	4	5	6	7
1. *C. wangyucheni* **sp. nov.**	**0.00 ± 0.00**						
2. *C. truncata*	10.10 ± 1.20	**0.07 ± 0.07**					
3. *C. bellua*	11.26 ± 1.30	8.49 ± 1.07	**0.56 ± 0.19**				
4. *C. clessini*	11.57 ± 1.30	7.62 ± 1.01	8.01 ± 1.40	**0.54 ± 0.24**			
5. *C. plicata*	11.72 ± 1.32	4.70 ± 0.85	8.93 ± 1.15	8.19 ± 1.03	**0.46 ± 0.17**		
6. *C. radiata*	12.96 ± 1.33	11.27 ± 1.24	11.85 ± 1.31	11.54 ± 1.23	10.21 ± 1.17	**1.02 ± 0.27**	
7. *C. "beirensis"*	13.17 ± 1.49	11.28 ± 1.47	12.32 ± 1.48	12.62 ± 1.44	10.76 ± 1.39	3.09 ± 0.74	**0.00 ± 0.00**

Table 3. Shell measurements of *Cristaria wangyucheni* sp. nov. Measurements in millimeters (mm).

Status of specimen	Specimen voucher	Shell length	Shell width	Shell height
Holotype	JXAU25039001	95.1	42.0	54.9
Paratype	JXAU25039002	71.1	25.0	45.8
Paratype	JXAU25039003	75.9	26.5	42.9
Paratype	JXAU25039004	105.9	42.8	61.9
Paratype	JXAU25039005	80.0	29.8	47.2
Paratype	JXAU25039006	87.8	29.5	52.5
Paratype	JXAU25039007	73.0	27.1	46.1
Paratype	JXAU25039008	62.5	26.0	41.8

(2025) may have been misidentified, despite its morphological similarity to that species. The classification of freshwater mussels is intricately linked to the geographic distribution of species, given the notable prevalence of endemism among them (Bolotov et al. 2020; Konopleva et al. 2023). It is noteworthy that *C. beirensis* was originally described from Beier Lake in northern China (Liu and Zhang 1982), whereas the two sequences in question were obtained from specimens collected in Sichuan in southern China. This discrepancy could also be attributed to insufficient sampling in phylogenetic reconstruction. Future studies should prioritize obtaining additional specimens of *C. radiata* from its type locality to clarify its taxonomic status.

Cristaria wangyucheni was discovered in a secondary tributary of the Jialing River Basin in the upper Yangtze River. The freshwater mussel diversity of this basin appears to be greatly underestimated. In addition to *Pseudocuneopsis sichuanensis* Huang, Dai, Chen & Wu, 2022 (Wu et al. 2022), several further species have recently been described from the region, including *Acudonta baitiaoensis* Wu, Liu & Zhang, 2025 (Wu et al. 2025), *Pseudocuneopsis perflora* Chen, Xiang, He, Huang & Wu, 2025, and *Tongchuania mingiana* Chen, Xiang, He, Huang & Wu, 2025 (Chen et al. 2025). Notably, the latter two species were also discovered in Dazhou City. Moreover, we have identified three additional freshwater mussel species from the upper Yangtze River that remain undescribed. Unfortunately, compared with previous survey results (Zeng et al. 1981; Zeng et al. 1985), our investigation suggests that freshwater mussels in the Jialing River Basin are at risk of extinction. We were unable to locate any live individuals of several yet undescribed species, and in most parts of the basin, only empty shells could be found. As the first major tributary of the Yangtze River to be fully channelized, the Jialing River has experienced a profound alteration of its hydrological conditions, with many sections transformed from lotic to slow-flowing or lentic habitats (Guo et al. 2022). Such environmental changes have likely caused the drastic decline or even extinction of most freshwater mussel populations in the region (Liu et al. 2020). These findings highlight the urgent need for systematic research and conservation efforts targeting the freshwater mussels of this basin.

Table 4. Analyzed conchological characters of *Cristaria* species.

Conchological features	*C. plicata*	*C. wangyucheni*	*C. beirensis*	*C. bellua*	*C. clessini*	*C. radiata*	*C. truncata*
Shell shape	Somewhat rhomboid	Irregularly ovate	Irregularly ovate	Somewhat trapezoidal	Irregularly ovate	Irregularly ovate	Somewhat rhomboid
Shell thickness	Thin	Thin	Thick	Generally thick	Generally thick	Thin	Thick
Shell color	Greenish-yellow or brownish-olivaceous	Yellowish green to brown	Black brown	Chestnut or blackish	Brownish	Yellowish green	Black brown
Umbo	Inflated, slightly higher than hinge line	Inflated, slightly higher than hinge line	Little inflated, low, slightly higher than hinge line	Slightly inflated, low	Inflated but low	Inflated, slightly higher than hinge line	Inflated, slightly higher than hinge line
Wing	High and border irregular	Wide and long	Degenerated	Small	Degenerated	Degenerated	High
Posterior ridge	High and rounded in young shells but nearly absent in older ones	Prominent but not sharp	Truncated	High, widely rounded	High, rounded, or somewhat biangulate	Rounded	Rounded
Surface sculpture	Faintly rayed in young shells and with strong posterior dorsal plication	With concentric square carving and a shallow sulcus in the middle of the dorsal margin	With regular growth lines	Posterior slope with a few folds; growth lines irregular	Posterior slope with a row of plications; growth lines irregular	Posterior slope with two conspicuous light and three dark rays	With regular growth lines
Nacre color	Dull whitish	Light white	Dull whitish	Blish-white, milky	Lurid, purplish-white	Lurid, white	Light orange

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